Nilsson, D-E., & Bok, M. J. (2017). Low-Resolution Vision-at the Hub of Eye Evolution. *Integrative and Comparative Biology*, *57*(5), 1066-1070. https://doi.org/10.1093/icb/icx120

OXFORD UNIVERSITY PRESS | Integrative and Comparative Biology

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Journal:	*Integrative and Comparative Biology*
Manuscript ID	ICB-2017-0115.R1
Manuscript Type:	Symposium Introduction
Date Submitted by the Author:	n/a
Complete List of Authors:	Nilsson, Dan-Eric; University of Lund, Department of Biology Bok, Michael; Vision Group, Department of Biology
Keywords:	eye evolution, vision, low resolution

SYMPOSIUM INTRODUCTION

Low-resolution vision - at the hub of eye evolution

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Synopsis Simple roles for photoreception are likely to have preceded more demanding ones such as vision. The driving force behind this evolution is the improvement and elaboration of animal behaviours using photoreceptor input. Because the basic role for all senses aimed at the external world is to guide behaviour, we argue here that understanding this 'behavioural drive' is essential for unravelling the evolutionary past of the senses. Photoreception serves many different types of behaviour, from simple shadow responses to visual communication. Based on minimum performance requirements for different types of tasks, photoreceptors have been argued to have evolved from non-directional receptors, via directional receptors, to low-resolution vision, and finally to high-resolution vision. Through this sequence, the performance requirements on the photoreceptors have gradually changed from broad to narrow angular sensitivity, from slow to fast response and from low to high contrast sensitivity during the evolution from simple to more advanced and demanding behaviours. New behaviours would only evolve if their sensory performance requirements to some degree overlap with the requirements of already existing behaviours. This need for sensory 'performance continuity' must have determined the order by which behaviours have evolved and thus been an important factor guiding animal evolution. Naturally, new behaviours are most likely to evolve from already existing behaviours with similar neural processing needs and similar motor responses, pointing to 'neural continuity' as another guiding factor in sensory evolution. Here we use these principles to derive an evolutionary tree for behaviours driven by photoreceptor input.

What is an eye and what is vision? From a human perspective, the answers may seem obvious, but considering the gradual evolution from non-directional light sensitivity, it is clear that we need functional criteria defining eyes and vision. The most fundamental property of an eye is its ability to simultaneously compare the light intensity in different directions. Another way of saying this is that an eye must divide the visual world into at least two pixels. To us, two pixels would not be sufficient to support any of our visually guided behaviours. But for a small worm or planktonic larva, two-pixel vision will offer new possibilities compared to a directional photoreceptor (single pixel) that only

delivers information when it is moved to scan the environment during locomotion. Natural selection that supports eyes in humans is rather different from the selection that once drove evolution from directional photoreception to the first cases of low-resolution vision. The morphological diversification tree that started with an ancient non-directional photoreceptor and gave rise to the enormous range of ocelli and eyes now distributed across the entire animal kingdom must thus have been driven by a corresponding evolutionary tree of behavioural tasks that provided the selection.

It is essential here to consider the causality in evolution of sensory systems (Nilsson 2013). All senses and associated nervous structures that acquire and process information about the external world are under selection to maximise fitness. But this fitness is generated directly by the success of the animals' behaviour, which in turn is generated by the senses and the nervous system. These, in turn, are generated by developmental processes, which are ultimately generated by expression of the genome. Obviously, the variation that selection works on follows the reverse causality, starting with the genome and ending with fitness. So even if the genome of course evolves under natural selection, the process follows a causal sequence from fitness to behaviour to sensory systems, to developmental mechanisms to the genome. In other words, behaviour is driving the evolution of sensory organs and nervous systems. Because of this 'behavioural drive', reconstruction of eye evolution should be based on a reconstruction of the evolution of the corresponding behaviours.

The evolution of behaviours is thus key for understanding the evolution of both senses and nervous systems in animals. The modification of a behaviour or the generation of a new one, requires coordinated changes at many levels. Just as the evolution of eyes was a long journey of numerous small adjustments from the first photoreceptor cells, the evolution of visually guided behaviour ~~was~~ started its long and winding road from simple circadian control of activity. ~~The important notion is that the evolution of behaviour is driving the evolution of sensory organs and nervous systems. Because of this 'behavioural drive', reconstruction of eye evolution should be based on a reconstruction of the evolution of the corresponding behaviours~~

This kind of reasoning was the basis for identifying a sequence of four classes of photoreceptive tasks, starting with *non-directional photoreception*, evolving first into *directional photoreception*, then into *low-resolution vision* and finally into *high-resolution vision* (Nilsson 2009; 2013). These four classes of sensory tasks were associated with specific behaviours. Low-resolution vision, which is the theme of the following seven papers in this issue, was defined as vision ~~associated~~ using ~~with~~ inanimate cues. All types of vision for seeing prey, predators or conspecifics were classified as high-resolution vision. The simplest low-resolution vision would require at least two pixels, but advanced forms may have thousands of pixels and a spatial resolution in the same range as some animals with high-resolution vision. It is thus not possible to use the degree of spatial resolution to firmly

distinguish between low and high-resolution vision. Most of the cases of low-resolution vision that have been studied so far have a spatial resolution in the range of 10°-40° (Chiussi and Diaz 2002; Nilsson et al. 2005; Garm et al. 2007; ~~Speiser and Johnsen 2008;~~ Yerramilli and Johnsen 2010; Speiser et al. 2011; Garm and Nilsson 2014; Petie et al. 2016).

Generally, seeing and interacting with other animals requires better resolution than that needed for using inanimate visual cues, but many small insects engage in high-resolution tasks, such as *Drosophila* performing visual communication with a resolution of about 6° (Ewing 1983; Gonzalez-Bellido 2011). It is important to note that the introduction of high-resolution vision in no way removes the benefit of low-resolution tasks. Behaving in response to inanimate cues serves behaviour in quite different ways compared to visual interaction with prey, predators and conspecifics. Practically all animals that use high-resolution vision also rely heavily on low-resolution tasks, often referred to as peripheral vision (Strasburger et al. 2011). In these cases, behaviours guided by inanimate cues (low-resolution vision) may use significantly higher spatial resolution than in animals that only have low-resolution vision (Wang et al.1997).

If we can establish an evolutionary tree of behaviours that relies on photoreceptor input, we will get a more detailed picture of low-resolution vision, how it arose from directional light-sensitivity and how it led to high-resolution vision. Such a tree would reveal the path that eye evolution took as well as the reasons for it. On which principles should such a tree of behaviours be constructed? For selection to drive the modification of a behaviour, the sensory receptors must already provide sufficient information to support the modified behaviour to some degree. Another way of saying this is that the performance of the receptor system must be within the performance range required for the modified behaviour. As an example, selection would not drive evolution of phototaxis if the available photoreceptors were too slow to allow any kind of useful phototaxis. Photoreceptors for circadian control may be very slow, with integration times of 5 minutes or more (Gotow and Nishi 2007), and this would not allow selection to introduce phototaxis of the type known from larval polychaetes (Jékely et al. 2008), which requires responses within a few seconds or less. The evolutionary change can still take place, but only if it proceeds via intermediate roles requiring intermediate response speeds.

For a photoreceptor, performance can be quantified not only by its response speed, but also by how small angles it measures light over, by the smallest intensity changes it can reliably detect, and by the wavelength range it is sensitive to. In other words, *response speed*, *acuity*, *contrast sensitivity*, and *spectral sensitivity* largely define the performance of a photoreceptor (for values, see Nilsson 2013). In some cases, *polarization sensitivity* is an additional performance factor. Evolution of any new behaviour based on photoreceptor input will thus require that there are already photoreceptors with

sufficient speed, acuity, and contrast sensitivity as well as a suitable spectral sensitivity to make the first tendencies towards the new behaviour result in improved fitness. As soon as selection favours development of the actual behaviour, there will be selection to change photoreceptor performance to not just be in the useful range, but to optimally support the new behaviour. This may in turn result in better photoreceptor performance, and open up for evolution of yet new and more demanding behaviours. If different behaviours call for very different optimal performance values, they may not be able to share input from the same photoreceptors, and that would favour duplication and subsequent divergence of photoreceptors.

The *performance continuity* described above is an absolute requirement for sensory evolution. As such, it can be used as a tool to infer the sequence along which photoreceptor-based behaviours evolved. But new behaviours will not only need sufficient photoreceptor performance. The neural circuitry will of course have to be modified, and different types of behaviours will require different types of sensory processing. From this it follows that a new behaviour is most likely to evolve from an existing behaviour with similar needs for sensory processing. Also the motor circuits needed to execute the new behaviour will have to rely on pre-existing similar circuits. On top of the performance continuity, there is thus also a requirement for *neural continuity* that has to be met when behaviours evolve.

A classification of behaviours based on the sensory tasks will naturally account for the neural continuity criterion, and performance continuity can then be used to organise the behaviours in each category into a probable sequence (Box 1). An evolutionary tree based on these criteria is displayed in Fig. 1. The transition from non-directional to directional photoreception is likely to have gone via shadow receptors or other faster photoreceptors bridging the gap in response speed from the slow receptors (Gotow and Nishi 2008) involved in circadian control. Accounting for related motor control and the need for a neural space map, directional photoreception, such as orientation toward contrasting objects, patterns or colours are likely to have originated as elaboration of simple (non-resolving) phototaxis. Also for similar processing needs, a continuation makes sense from low-resolution orientation and course-control behaviours to all the high-resolution behaviours involving detection, pursuit and interaction between animals. Posture control (optical statocysts) and protective responses (e.g. shell closure in bivalves or withdrawal in fan worms) seem more likely to be dead ends because of their need for direct neural lines with minimal processing, and also very different motor responses (see Bok et al. 2016; Speiser and Johnsen 2008). Even though there are evolutionary paths that appear more likely than others, there may of course be unusual conditions that make other paths possible.

We do not claim that the conclusions presented here are anything but suggestions, but together with molecular cues and developmental homologies, the principles outlined here are essential for reconstructing the evolution of visually guided behaviours and visual systems. Different paths may have been taken in different animal groups, and it is of interest to include model systems with a variety of life styles from all corners of animal phylogeny. Outside the well-studied vertebrates, arthropods and cephalopods, photoreceptor-driven behaviour has been studied in animal groups such as box jellyfish, sea urchins, starfish, gastropods, chitons, bivalves, and fan worms (Garm et al. 2007, 2011; Garm and Nilsson 2014; Petie et al. 2016; Chiussi and Diaz 2002; Ziegler and Meyer-Rochow 2008; Boyle 1972; Speiser and Johnsen 2008; Wilkens 1986; Soo and Todd 2014; Nilsson 1994). Clearly, there are already a number of good models at key positions in the evolution of visually guided behaviours (Fig. 1). At this level of detail, the emerging pattern is simple. High-resolution vision, such as our own, seems firmly rooted in different types of optical taxis behaviours, making low-resolution vision central for eye evolution.

Funding

This work was supported by grants to D.-E. N. by the Knut and Alice Wallenberg Foundation and the Swedish Research Council.

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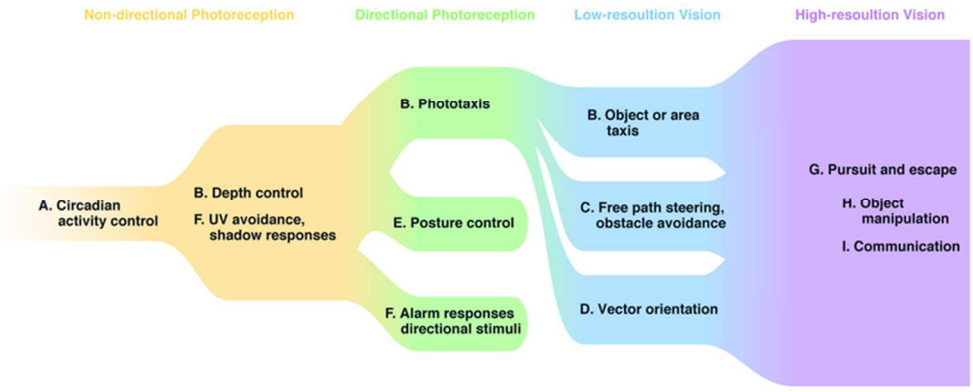
Fig. 1 Evolution of behaviours driven by photoreceptor input. The diagram only shows major paths, and is colour coded according to the four levels of sensory tasks introduced by Nilsson (2009, 2013). Note that behaviours to the left in the diagram may remain relevant even after more complex behaviours have evolved in the same animal. Modifications leading to one or more new types of behaviours in the left half of the diagram often call for divergence of photoreceptor types and new organs with photoreceptors. Behaviours on the right side instead tend to share the same lateral cephalic organs (eyes). Behaviours based on high-resolution vision may arise by combinations of neural circuits originally evolved for different low-resolution behaviours.



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Box 1. Classification of behaviours guided by photoreceptor input

To leave evolutionary links to high-resolution vision open, we place these in their own 'Advanced' category. Roman numerals indicate behaviours based on (I), non-directional light sensitivity; (II), directional light sensitivity; (III), low-resolution vision; (IV), high-resolution vision.

A. (I) **Circadian activity control -** behaviours initiated, terminated or otherwise controlled by the ambient light intensity or being under influence of an endogenous rhythm entrained by the ambient intensity (periods could also be lunar or annual)

B. Taxis behaviours - habitat positioning by locomotion toward or away from directions with particular optical signatures associated with good opportunities for feeding or mating, or low risks for predation

- (I) Depth control in water
- (II) Phototaxis without spatial resolution
- (III) Object or area taxis (attraction or repulsion to resolved objects, or to areas with specific distribution of luminance, colour or polarization)

C. Course negotiation in a 3-D environment - steering to follow a suitable path in relation to nearby structures

- (II) Exposure responses in burrowing animals (to avoid or aim at breaking through substrate surface)
- (III) Steering behaviour to find free way and avoid obstacles

D. Vector orientation behaviours - habitat positioning by straight locomotion in relation to cues that are neither attractive nor repulsive (landmarks or celestial cues)

- (III) Orientation (to maintain a vector, i.e. for getting out of an unfavourable area or avoid depleting a food source)
- (III) Migration behaviour

E. Posture control - behaviours aimed at orienting the body in relation to the environment

- (II) Body orientation using optical statocysts (supported by nauplius eyes in crustaceans or dorsal ocelli in insects)
- (III) Body orientation using low-resolution vision. This may develop from habitat positioning behaviours rather than from behaviours associated with optical statocysts

F. Protective responses to luminance changes - locomotion or other responses to avoid an optically detected threat

- (I) Avoidance of harmful radiation levels (UV/blue) by sinking in the water column
- (I) Non-directional shadow responses
- (II) Alarm responses to directional luminance changes (Clinching, withdrawal or shell closure responses)

Advanced behaviours

G. (IV) **Pursuit and escape behaviours, visually guided foraging - locomotion in relation to prey, other food items, predators, or conspecifics**

H. (IV) **Object manipulation (e.g. for nest building)**

I. (IV) **Communication with other animals**